

LIFE CYCLE, DEMOGRAPHY, AND REPRODUCTIVE  
BIOLOGY OF HERB ROBERT (*GERANIUM  
ROBERTIANUM*)

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**ABSTRACT.** For nine years I studied the life cycle, demography, and reproductive biology of a woodland herb, *Geranium robertianum*, in central Massachusetts. These plants are facultative biennials that typically flower in the year after germination. Of 408 seeds experimentally sown in natural habitat, 26% gave rise to seedlings within six years. Of 1352 marked, naturally occurring seedlings, 53% survived to the end of their first growing season, 13% of plants alive at the end of their first growing season survived to year two, and 54% of these flowered. Plants germinating in early spring were more likely to survive to the end of year one and to flower than those germinating later in the year. Low summer rainfall appeared to reduce summer survival and low winter temperatures combined with little snow cover seemed to reduce winter survival. Floral structure and development, pollen-ovule ratios, and pollinator activity all suggest that plants of this species are highly self-pollinated. Herb Robert is one of only a few biennials that occupy undisturbed forest habitat.

**Key Words:** biennial, demography, facultative biennial, *Geranium robertianum*, herb Robert, life cycle, life history, self-pollination

Biennials are rare, comprising only 1.4% of the 14,500 species in the provisional checklist of the Flora of North America (Hart 1977). Plants with this life cycle pattern often are said to be associated with disturbed habitats (Kelly 1985; Silvertown 1984), although a few biennial herbs of relatively undisturbed habitats, such as forests, are known (Morgan 1971).

Numerous hypotheses have been proposed regarding the adaptive significance of bienniality (Bender and Baskin 1994; Hart 1977; Meidjen et al. 1992; Schaffer and Gadgil 1975; Silvertown 1984), but our current knowledge of biennial species is insufficient to decide which, if any, of these hypotheses is correct. Given this state of knowledge, examination of the natural history of additional biennial species is desirable.

Here I present an ecological investigation of a putative biennial, *Geranium robertianum* L. (herb Robert, Geraniaceae), emphasizing the species' life cycle and two areas potentially relevant

to interpreting the life cycle: demography and reproductive biology. My specific objectives were to 1) determine what life cycle pattern this species possesses; 2) understand the timing and causes of mortality; 3) investigate the relationship between germination time, vegetative growth, and flowering; and 4) describe the flowering phenology and breeding system.

*Geranium robertianum* is a forest herb that has been referred to as a biennial, but also as an annual, a winter annual, and a monocarpic or polycarpic perennial (Baker 1956; Falinska and Piroznikow 1983 and references therein; Fernald 1950; Gleason and Cronquist 1991; Widler-Kiefer and Yeo 1987; Yeo 1973). Even within North America, the species has been described as an annual (Fernald 1950), an annual or winter annual (Great Plains Flora Association 1986), and an annual or biennial (Gleason and Cronquist 1991).

Herb Robert occurs in northeastern North America, Eurasia, and northern Africa (Baker 1957; Widler-Kiefer and Yeo 1987). The North American range extends from Newfoundland to Maryland, west to Illinois (Fernald 1950). The species has been introduced to western North America, New Zealand, and Singapore (Baker 1957).

Herb Robert typically occurs in shady or partly shaded habitats, and often is associated with rocky ground and nutrient-rich or basic soils (Baker 1956; Falinska and Piroznikow 1983; Voss 1985). In North America, the habitat of herb Robert is described as “damp rich woods” (Gleason and Cronquist 1991), “rocky woods, ravines and gravelly shores” (Fernald 1950), and “rich deciduous woods . . . clearings, along roads and trails . . . rocky openings, gravelly shores and rubble” (Voss 1985). In New England the species is listed as “occasional” by Seymour (1969). It is absent from several Massachusetts coastal counties and is rare in Rhode Island (George 1996; Sorrie and Somers 1999). In central Massachusetts, the species occurs sporadically and is restricted largely to rocky wooded slopes with soils that are seemingly richer and/or less acid than the norm.

#### MATERIALS AND METHODS

**Field work.** I conducted field work at two sites in Princeton, Massachusetts (42°28'N, 71°54'W). Herb Robert plants at both sites grew among boulders in rocky woodland. Because much of

the ground surface was occupied by boulders, plots were placed arbitrarily rather than randomly to avoid including large areas of unvegetated rock.

One study site was at an elevation of 350 m on a south-facing slope in Wachusett Meadow Wildlife Sanctuary of the Massachusetts Audubon Society. Dominant trees at this site were shagbark hickory [*Carya ovata* (Miller) K. Koch], white ash (*Fraxinus americana* L.), and sugar maple (*Acer saccharum* Marshall), with hornbeam [*Ostrya virginiana* (Miller) K. Koch] common in the understory. Two plots were arbitrarily selected on this slope in the spring of 1990. Plot A occupied 0.72 m<sup>2</sup> with little vegetation other than herb Robert present. Plot B was 12 m from plot A, comprised 1.82 m<sup>2</sup>, and contained a fern [*Dryopteris marginalis* (L.) A. Gray], Virginia creeper [*Parthenocissus quinquefolia* (L.) Planchon] and the goldenrod *Solidago caesia* L.

The second site was 2.7 km from the first site, in Wachusett Mountain State Reservation, at an elevation of 430 m. The dominant woody plants on this ESE-facing slope were white ash, sugar maple, shagbark hickory, hornbeam, red elderberry (*Sambucus racemosa* L.), and alternate-leaved dogwood (*Cornus alternifolia* L.f.). Plot C, established in 1990, was 0.82 m<sup>2</sup> and contained Jack-in-the-pulpit [*Arisaema triphyllum* (L.) Schott.], enchanter's nightshade (*Circaea lutetiana* L.), and fringed bindweed (*Polygonum cilinode* Michx.). A second plot (D) was established at this site in 1995 to increase the number of plants being monitored. It included little vegetation besides herb Robert.

Plots were visited starting in late April or early May in each year between 1990 (1995 for plot D) and 1998. The plots were visited weekly until late June and at two- to three-week intervals thereafter until late September or early October. I also visited the plots four times in 1999 to determine the fate of the 1998 cohort. Newly germinated plants were recognized by their cotyledons and small size. Each was monitored throughout its life following marking with a numbered plastic stake secured to the plant with a plastic twist tie. During each visit I recorded the number of leaves on each plant as an indicator of plant size. For reproductive plants, I recorded the numbers of flowers and fruits and used the maximum recorded sum of flowers and fruits as a conservative estimate of total flower production for each plant. Substrate depth was measured for each plant at the time of its death by pressing a plastic knitting needle marked in 1 cm increments down into

the humus at the base of the plant until it reached a rock or a depth of 12 cm. The length of the concealed portion of the needle was taken as the substrate depth.

To examine the demography of dispersed seeds, I sowed seeds into twelve 60 cm diameter plots at Wachusett Meadow in 1993. Plots were chosen on the same rocky hillside as plots A and B, and the center of each was marked with a numbered plastic stake. Each seed demography plot was at least 2.0 m from the nearest herb Robert plant to minimize the possible presence of any naturally occurring herb Robert seeds, but was in habitat that appeared to be appropriate for the species. Seeds were collected from naturally growing plants at Wachusett Meadow and sown in the plots. Each plot received 10 seeds on July 14, 7 on July 16, 9 on July 19, 4 on July 25, and 4 on August 8, for a total of 34 seeds. The variation in these numbers reflects the natural variation in seed supply during the summer. Seeds were scattered on the surface of the leaf litter, as they would be during natural dispersal, within 30 cm of the center of the plot. The plots were monitored for seedlings at 1–3 week intervals during the remainder of the 1993 growing season and in each of the 1994–1998 growing seasons, and four times during 1999. The area between 30 cm and 150 cm from the plot center also was monitored during these visits to detect any additional seedlings that might suggest the presence of a naturally occurring seed bank in or near these plots.

I made field observations of floral development and pollinator activity using 38 marked flowers on a total of twelve plants near plots A and B in early June, 1993 at Wachusett Meadow. I collected one flower from each of five plants at each site to determine pollen/ovule ratios (see below).

Information on weather conditions was obtained from two locations. Temperature and precipitation records were obtained from the weather station at the Worcester airport. This station is 300 m above sea level and 22 km S of the study sites. I obtained daily records of winter snow cover from this station until October, 1995 when the weather station ceased recording this information. From October, 1995 through April, 1999 snow cover records were recorded at the author's residence in Paxton, Massachusetts, 15 km SSW of the study sites, at an elevation of 318 m.

**Laboratory studies.** Seeds from the Princeton, Massachu-

setts populations were unavailable when laboratory investigations were conducted; instead I used eight plants established from seeds collected in Hinesburg, Vermont. Plants were grown in 8 cm square pots containing Metromix 350, a soil-less growth medium. Plants were overwintered in a greenhouse at a temperature just above freezing, and were then moved to a growth chamber for further study. The temperature in the chamber was 25°C during each 14 hr. day and 15°C during each 10 hr. night.

The ability of flowers to self-pollinate was examined in a growth chamber in the absence of insects. I used four experimental treatments: 1) hand self-pollination, 2) hand cross-pollination, 3) no pollination, and 4) emasculation and no pollination. Treatments were assigned randomly within two or three blocks of four flowers on each of eight plants. The stigmas of hand-pollinated flowers received large loads of pollen from a toothpick on all five stigmas. Emasculation involved removing anthers with fine forceps shortly after the flowers opened. Any pollen inadvertently deposited on stigmas was removed by wiping with moist cotton under a dissecting microscope. Seeds were counted at fruit maturation.

One flower from each of four Vermont plants was collected and, in addition to the five flowers from each Massachusetts site, used to determine pollen/ovule ratios. The number of ovules in each flower was counted under a dissecting microscope. One anther from each flower was emptied into a small Petri dish containing 70% alcohol and the pollen grains, which are large in this species, were counted over a 2 mm × 2 mm grid using a dissecting microscope.

**Data analysis.** Sample sizes from individual field plots were too small for most analyses, so I lumped data for all four plots. This lumping violates the assumption of independence of observations, and this shortcoming should be considered in interpreting results. However, general trends were usually similar in the four plots. For example, correlations between plots A, B, and C in numbers of seedlings over nine years were all significantly positive ( $r > 0.67$ ,  $P < 0.05$ ). No correlations between plot D and the other plots were significant, though these tests were not very powerful because I had only four years of data for this plot.

I used three kinds of analyses for field data. I used G-tests to evaluate independence of variables for frequency data (e.g., num-

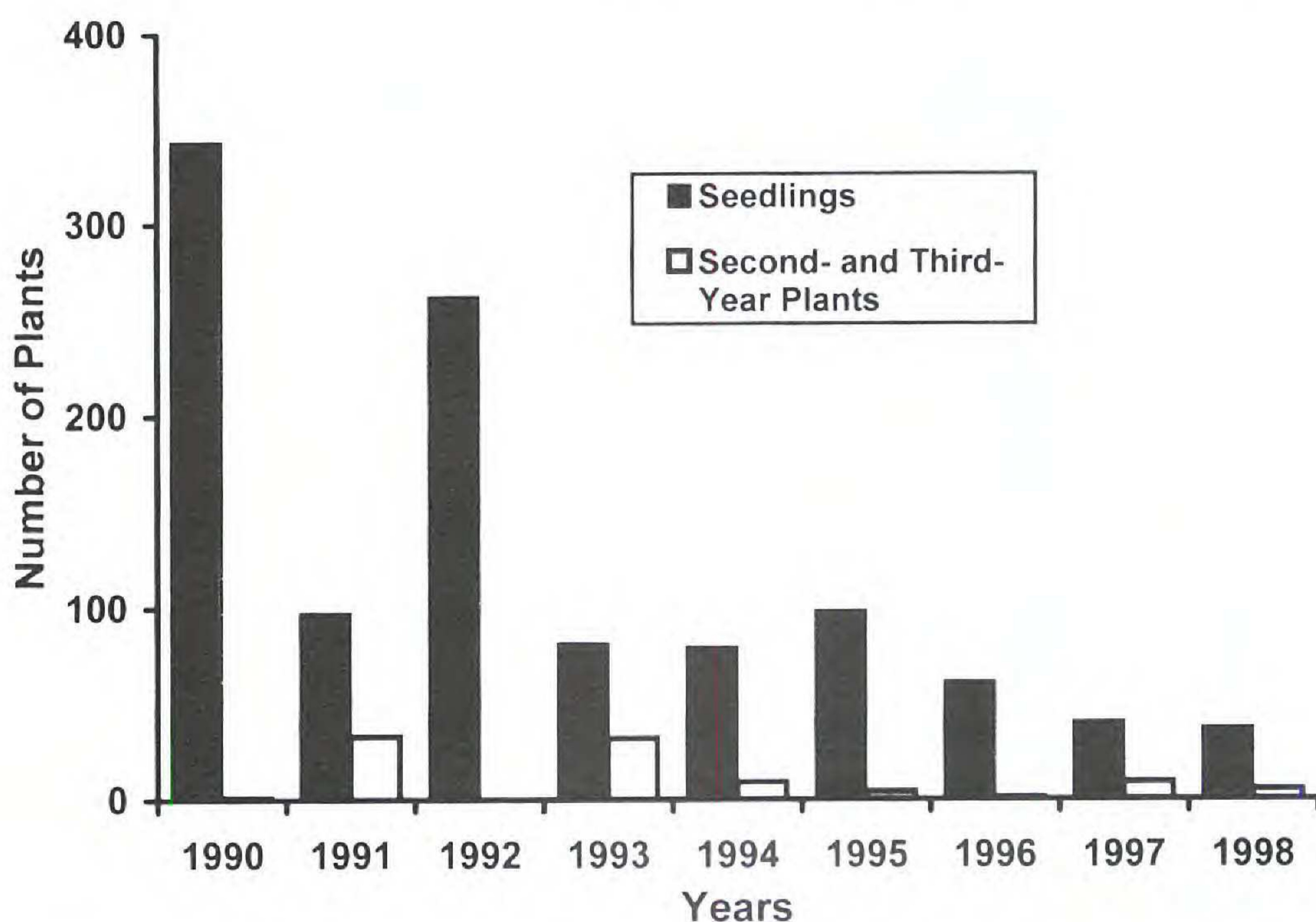


Figure 1. Numbers of seedlings and older (2nd- and 3rd-year) plants in plots A–C in nine years. Second and third year plants represent survivors from earlier years.

ber of survivors and non-survivors in different years). I used product-moment correlations to evaluate associations between continuous variables, such as proportion surviving and amount of precipitation in different years. Finally, I used a t-test to compare the numbers of flowers produced by early- and late-emerging seedlings.

## RESULTS

**Plant demography.** A total of 1352 seedlings was marked between 1990 and 1998, and each seedling was monitored for its entire life. Considering just plots A–C, which were monitored for the entire study, the numbers of emerging seedlings varied from 37 in 1998 to 343 in 1990 (Figure 1). Numbers of older (2nd- and 3rd-year) plants also varied dramatically among years, from one plant for plots A, B, and C combined in 1992 to 34 plants in 1991 (Figure 1). Emergence was concentrated in May, especially, and June, but continued at a low level through October (Figure 2).

Of the 1352 marked seedlings, 53% survived until the end of

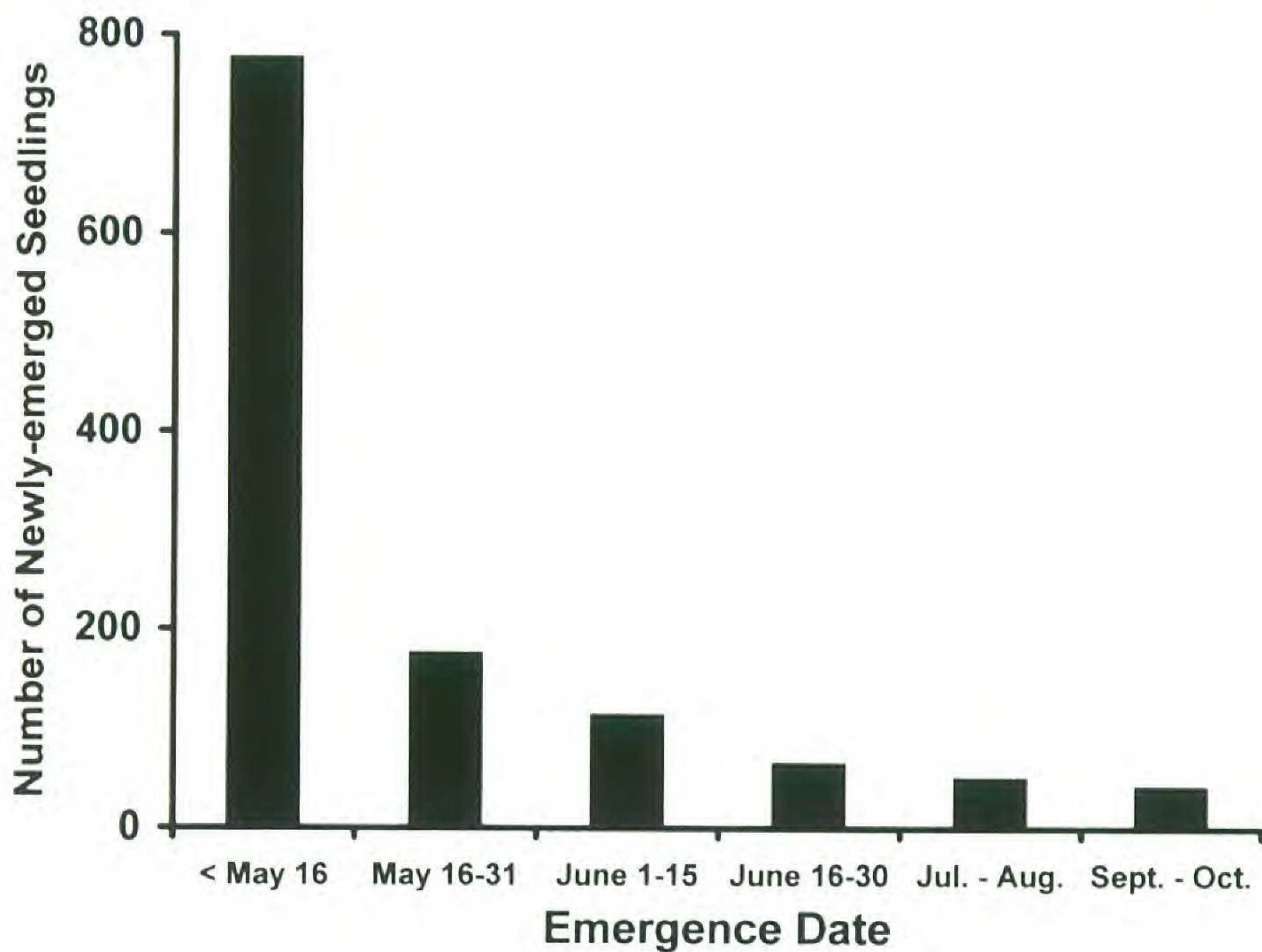


Figure 2. Numbers of newly emerged seedlings at different times of the year. Data are combined for plots A–D and for years 1990–1998.

the first growing season and 7% survived their first winter and produced at least one leaf the following year (Figure 3). Of the 98 plants surviving their first winter, 51% flowered during the second year and subsequently died, 30% died during their second year without flowering, and 14% died during the subsequent winter. The remaining 5% did not flower during their second year, but survived to their third year. Of these five individuals, three flowered and died during their third year and two died without flowering. In all, 53 of the 1352 marked individuals flowered at some time, 50 (94%) in their second year and three in their third year.

**Yearly differences in survivorship.** Survival of seedlings through their first growing season and first winter varied considerably from year to year (Figure 4). Survival of seedlings to the end of their first year varied from 5.5% ( $n = 109$ ) in 1995 to 65.7% ( $n = 201$ ) in 1996. Overwinter survival ranged from 0.0% ( $n = 59$ ) in 1991 to 21.3% ( $n = 150$ ) in 1992. G tests for independence of year and survival revealed significant departures from independence both for seedling survival during the first growing season ( $G = 148.48$ , 8 df,  $P < 0.001$ ) and the first winter

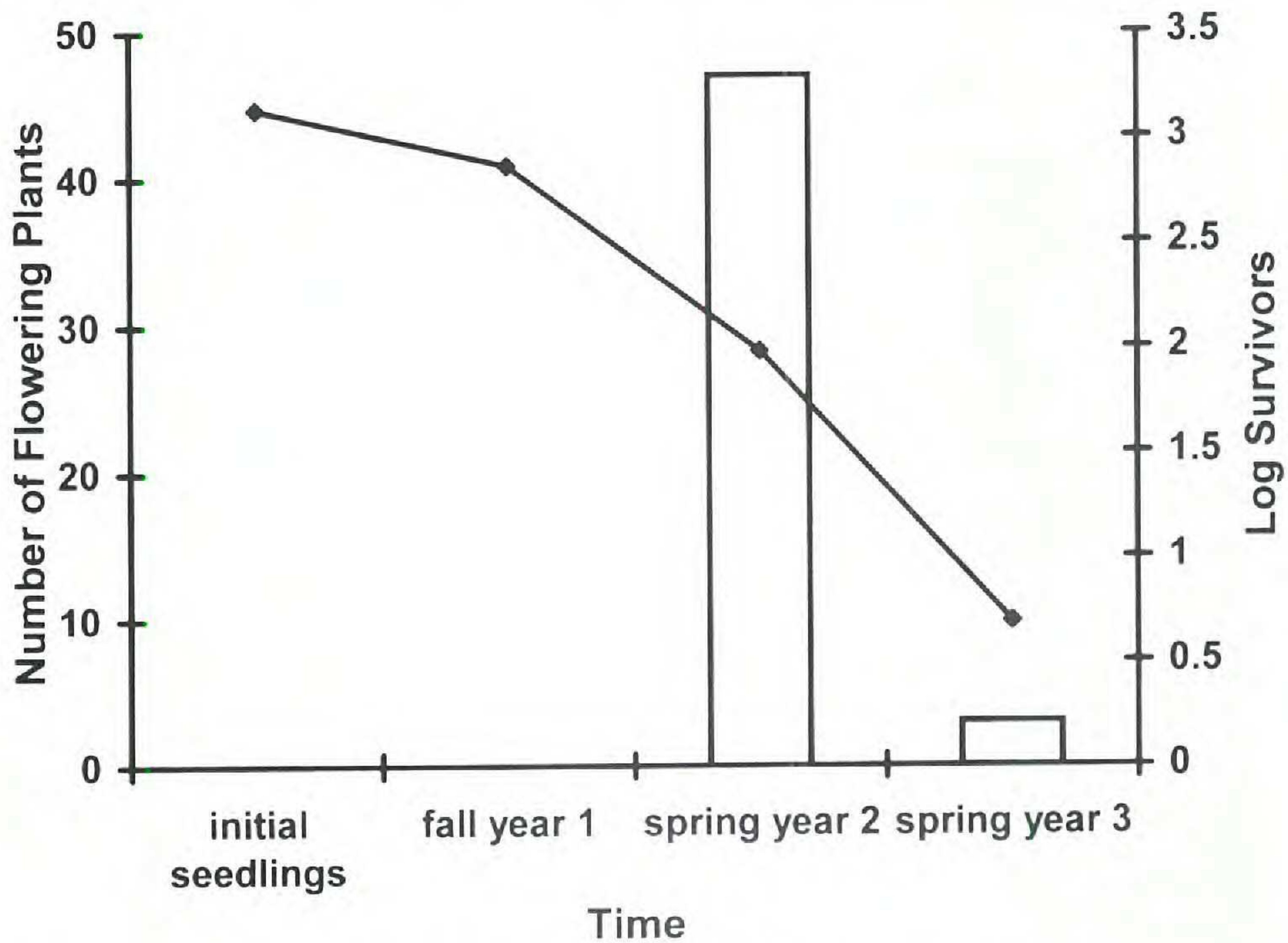


Figure 3. Survival and flowering of 1352 plants marked as seedlings in plots A–D during the years 1990–1998. Survivorship for years 2 and 3 was measured at the beginning of the year. No plants survived to year 4.

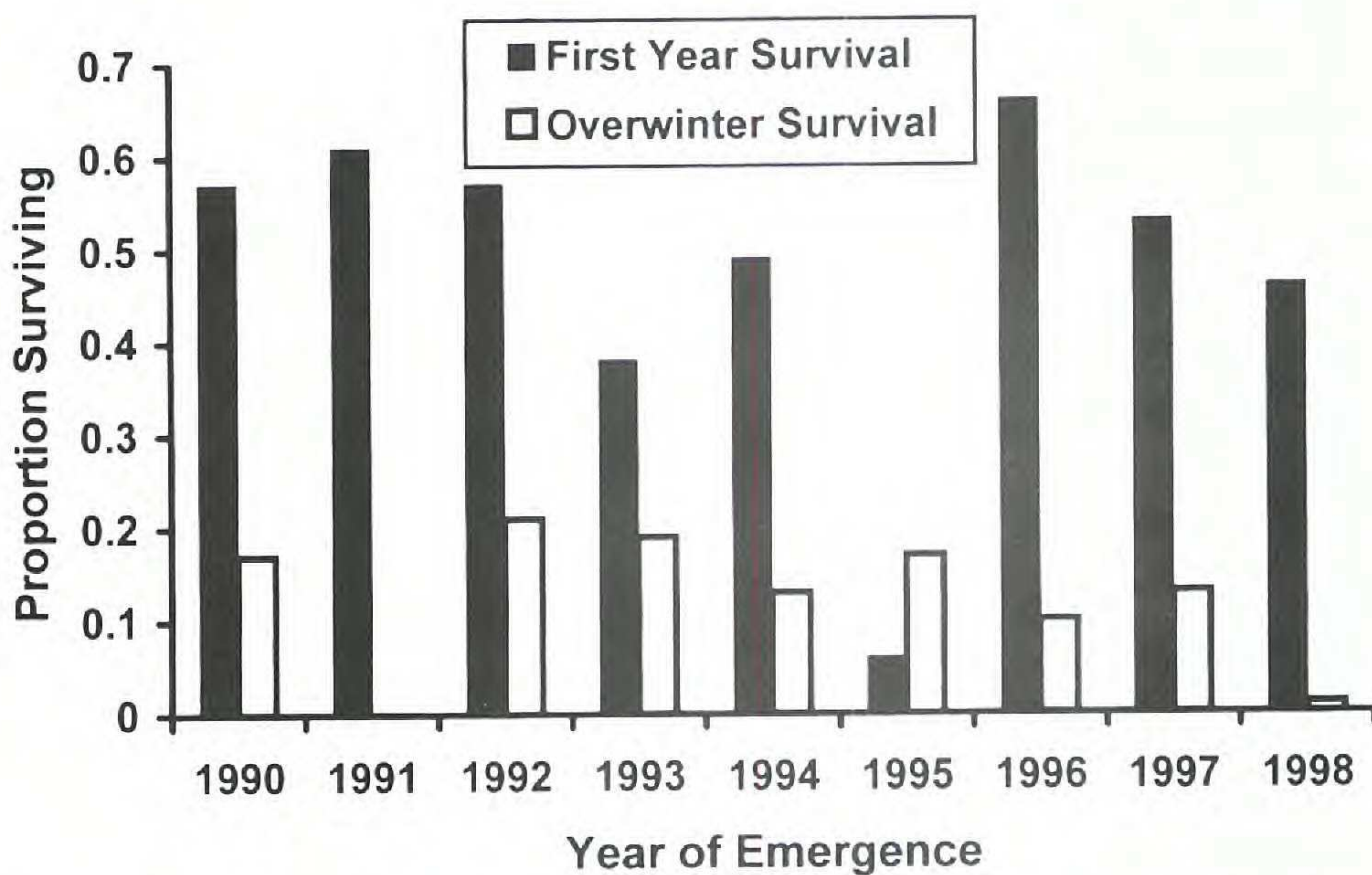


Figure 4. Yearly variation in survival of seedlings emerging in nine years. Data for plots A–D are combined. Overwinter survival is the proportion of plants alive at the end of their first year that survived to spring of the following year.



( $G = 44.46$ , 4 df,  $P < 0.001$ ). The second analysis has fewer degrees of freedom than the first because it excludes four years of data for which the expected values were below 5.0.

The yearly differences in survival seem in part to reflect prevailing weather conditions, especially precipitation during the summer, and temperature and snow depth during the winter. Survival of seedlings to the end of their first year was positively correlated (though not significantly so,  $P > 0.05$ ) with the amount of precipitation in May ( $r = 0.46$ ), June ( $r = 0.57$ ), and August ( $r = 0.36$ ), but not in July ( $r = -0.15$ ). Survival was, however, significantly correlated with the amount of precipitation in May–July and May–August ( $r = 0.68$ ,  $0.74$ , respectively,  $P < 0.05$ ). The lowest rainfall for any of these months in the nine years of the study was in June of 1995, when only 3.8 cm of rain fell, 42% of the June average. Over 94% of seedlings died by the end of this year, compared to a nine-year average mortality of 52%.

Overwinter survival of plants alive at the end of the first growing season was positively correlated with total winter snowfall ( $r = 0.52$ ), although not significantly so ( $0.20 > P > 0.10$ ). The winter with greatest survival was 1992–93, which also had a greater snowfall than any winter in the preceding century (3.1 m). If exposure to harsh winter conditions reduces survival, it would seem that a combination of low winter temperatures and minimal snow cover would be more highly correlated with winter mortality than snow cover alone. This is suggested by the nearly significant negative correlation ( $r = -0.64$ ,  $0.10 > P > 0.05$ ) between survival and the number of winter days with both temperatures below  $-12^{\circ}\text{C}$  ( $10^{\circ}\text{F}$ ) and less than 2.5 cm (1 in.) of snow cover. The winter with the lowest survival (1991–92, 0% survival) also had the largest number of such cold days with bare ground (15, compared to 1–7 in other years).

The substantial variation in numbers of seedlings emerging in different years caused the density of seedlings to vary dramatically among years and plots (range = 1–191/m<sup>2</sup>). This density was not, however, related to survival or flowering. Correlation coefficients between seedling density and survival to the end of the first year, overwinter survival, and proportion of overwinter survivors that flowered were 0.23 ( $n = 31$ ),  $-0.05$  ( $n = 29$ ) and 0.45 ( $n = 15$ ), respectively.

**Performance of seedlings.** Emergence date was strongly as-

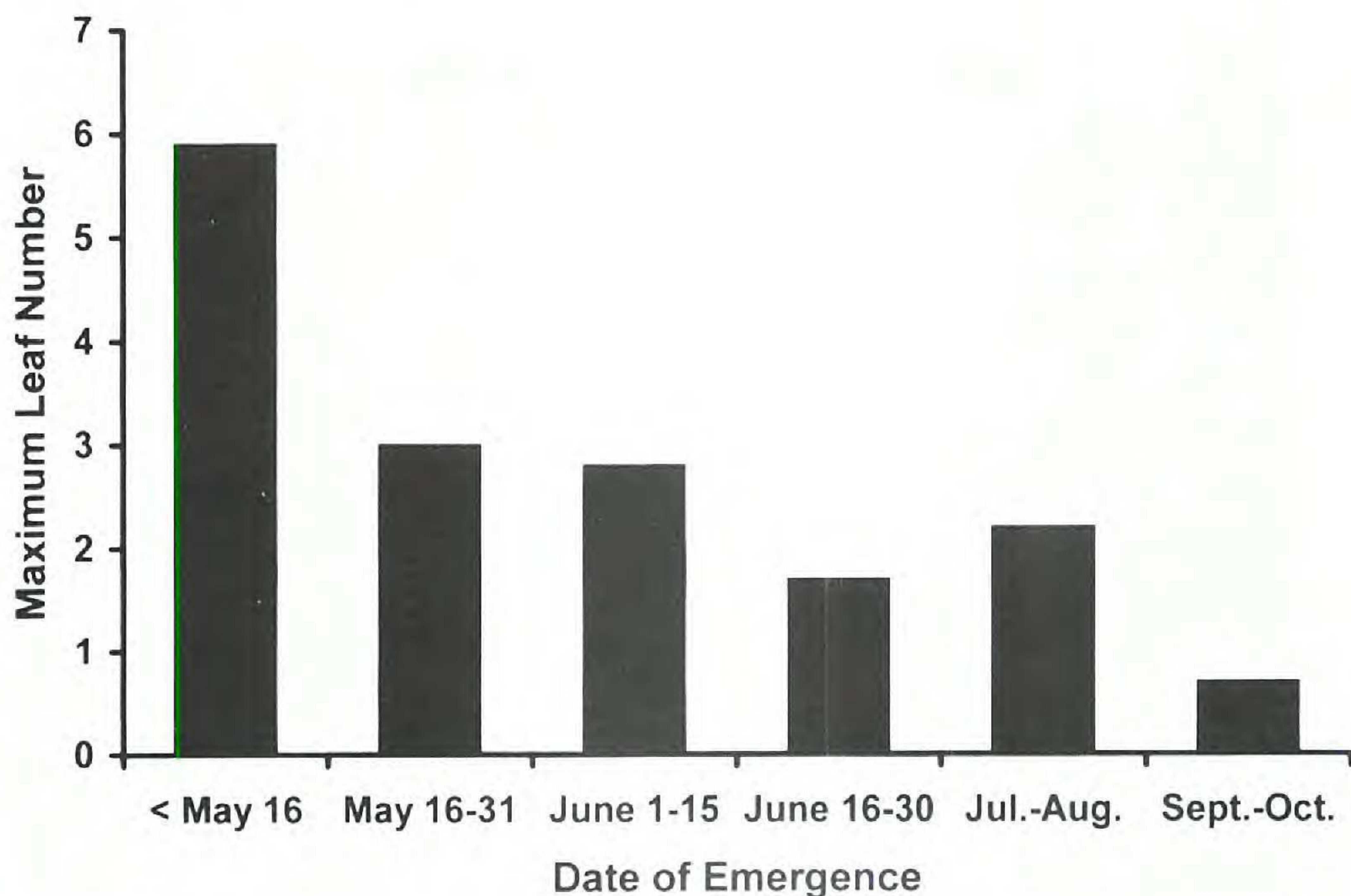


Figure 5. Average maximum leaf numbers produced during their first year by plants emerging at different times of the year.

sociated with the size (as represented by maximum leaf number) attained by first year plants, with their likelihood of surviving to the end of the first growing season, and with the numbers of flowers that they produced. Plants emerging in late April and the first half of May bore an average maximum of 5.9 leaves during their first season, while the average maximum number for the other time intervals was no more than half this number (Figure 5). Plants emerging on or before May 15 had a 56% chance of surviving to the last census date of the year, while the probability for those emerging after May 15 was 0.36. This latter figure was inflated by the high survival of seedlings that emerged in September and October (0.93), reflecting the fact that many of them needed to survive for only 2–3 weeks to live to the end of the growing season.

Plants surviving to the end of the first season had a slightly greater chance of surviving the winter if they emerged on or before May 15 than if they emerged later in the year (18% vs. 11%;  $G = 4.46$ , 1 df,  $P < 0.05$ ). However, if seedlings emerging in September and October are excluded, the survival of late-emerging seedlings increases to 14%, which is not significantly different from 18% ( $G = 1.20$ , 1 df).

Of plants surviving to year two, a much greater percentage of those that emerged as seedlings by May 15 flowered than did those that emerged after that date (62% vs. 17%;  $G = 13.14$ , 1 df,  $P < 0.001$ ). Furthermore, among plants that flowered, those from early-emerging seedlings ( $\leq$  May 15) produced over three times as many flowers as late-emerging seedlings (18.7 vs. 5.0; SE = 2.59, 1.67;  $n = 48, 5$ ). This difference between means is significant based on log-transformed data ( $t = 3.07$ ,  $P < 0.01$ , 51 df).

Plant size attained during a plant's first year influenced the probability of overwinter survival and flowering. Plants alive at the end of their first year and with a maximum leaf number of 3–9 had a 16% chance of surviving the winter, compared to an 8% chance for plants with both fewer (0–2) and more (10+) leaves (G-test for independence,  $G = 13.42$ , 2 df,  $P < 0.01$ ). Among plants surviving to year two, those bearing 0–2 leaves in their first year had a 33% chance of flowering, compared to a 54–60% chance for plants with 3–9 and 10+ leaves, though the sample sizes were too small to test for independence. Among plants that flowered, the maximum leaf number showed a modest but significant correlation with flower number ( $r = 0.41$ ,  $n = 53$ ,  $P < 0.05$ ).

Substrate depth had a modest but significant effect on seedling survival to the end of the first growing season, with seedlings occupying substrates of intermediate depth (3 cm) having the highest survival (G-test for independence,  $G = 15.18$ , 5 df,  $P < 0.001$ ; Figure 6). Substrate depth had no effect on overwinter survival of those plants surviving to the end of the first growing season ( $G = 2.92$ , 4 df, ns), nor on the flowering of those plants surviving until the start of the second growing season ( $G = 6.50$ , 4 df, ns).

**Seed demography.** Of the 408 seeds sown into the 12 seed demography plots, 105 emerged within six years, the majority in the year after sowing (Figure 7). At the conclusion of observations, 74% of the original seeds had not emerged, having either died or remained in the soil seed bank. No seedlings were observed within 1.5 m of the marker stakes except for those within 0.3 m of the stakes and presumably sown by me. Thus there is no evidence that the results were confounded by the presence of a naturally occurring seed bank.

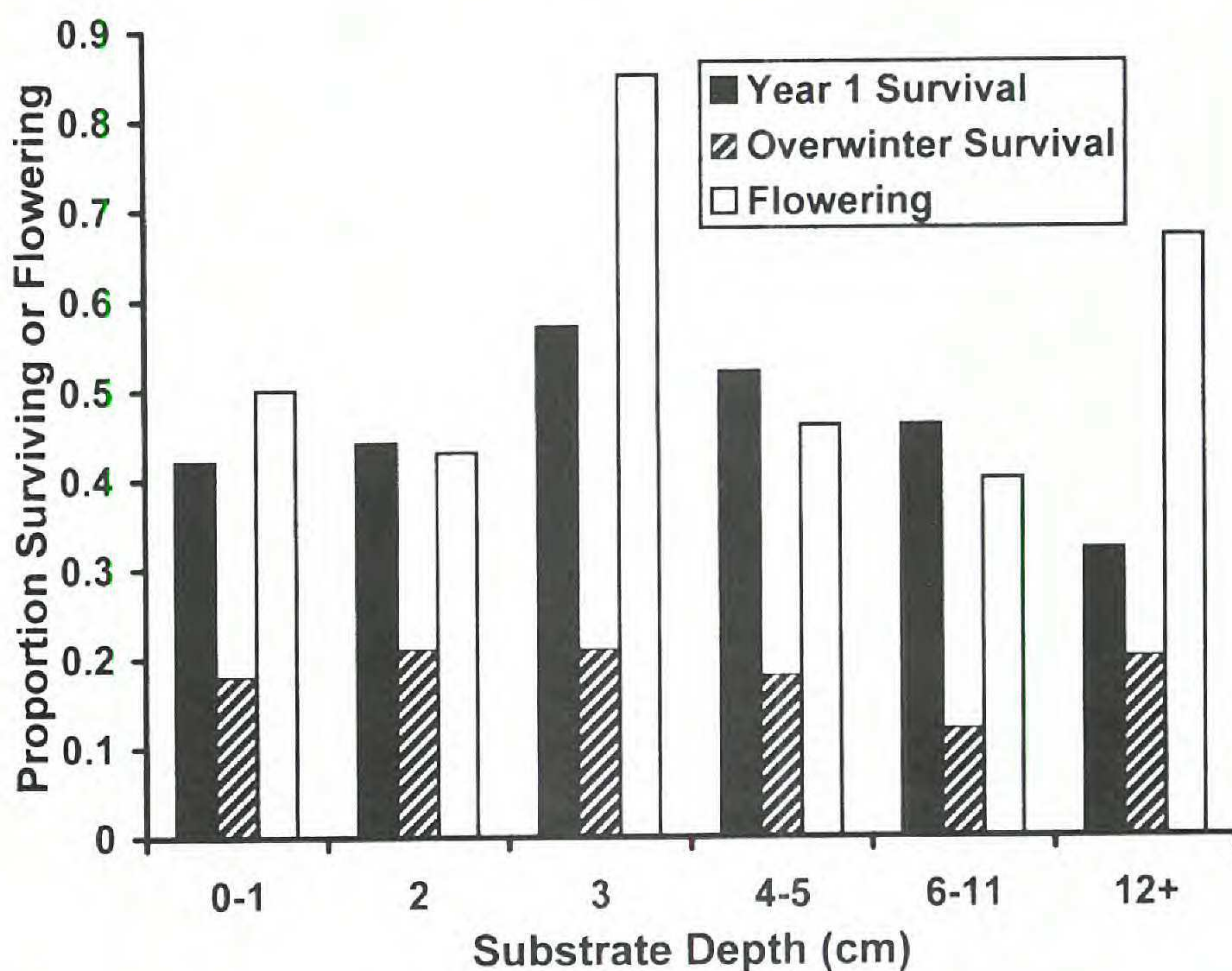


Figure 6. Influence of substrate depth on proportion of plants surviving and flowering. Proportions are calculated as in Figure 7. Data are combined for plots A–D.

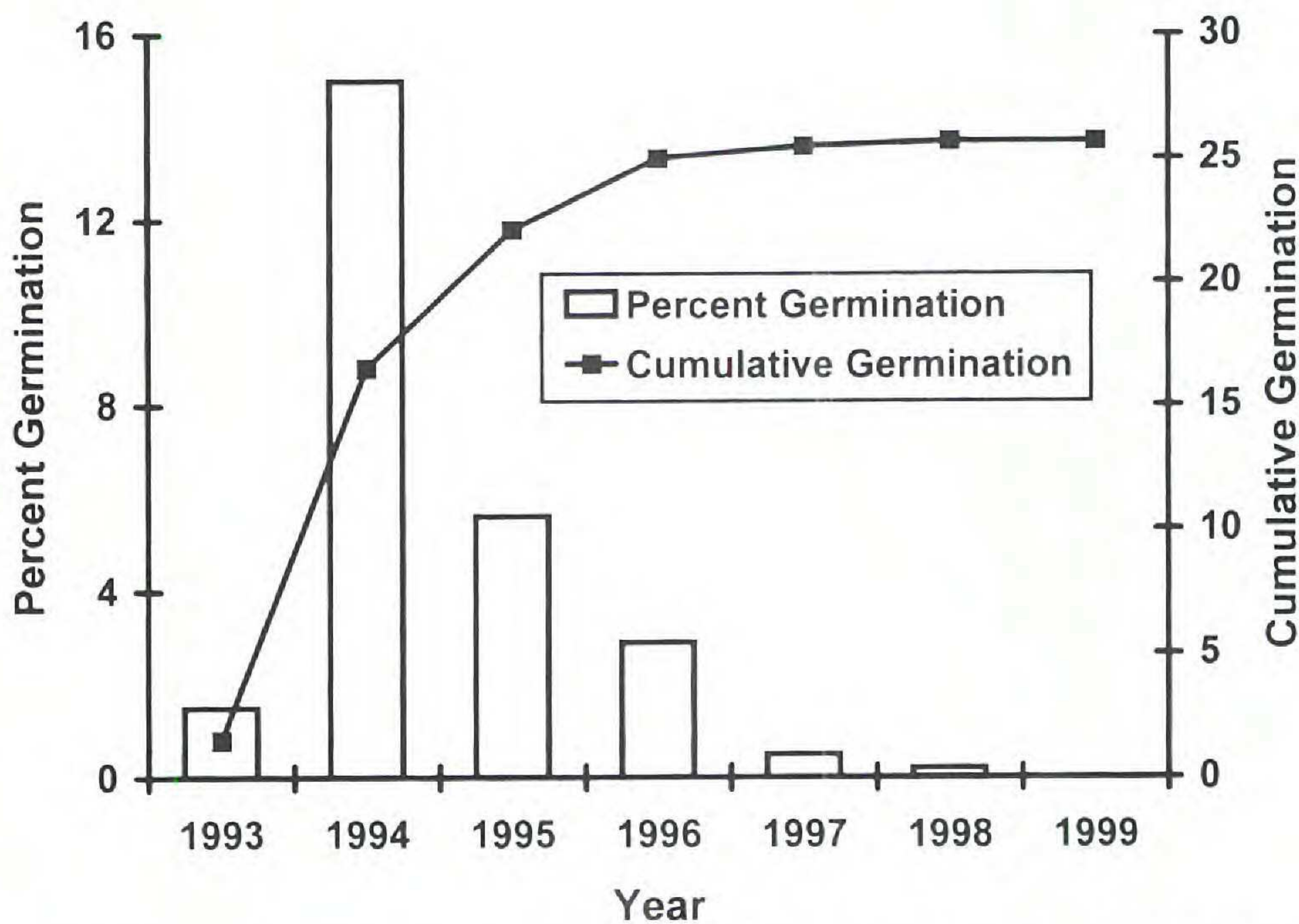


Figure 7. Temporal pattern of emergence of 408 seeds sown in 12 plots during the summer of 1993.

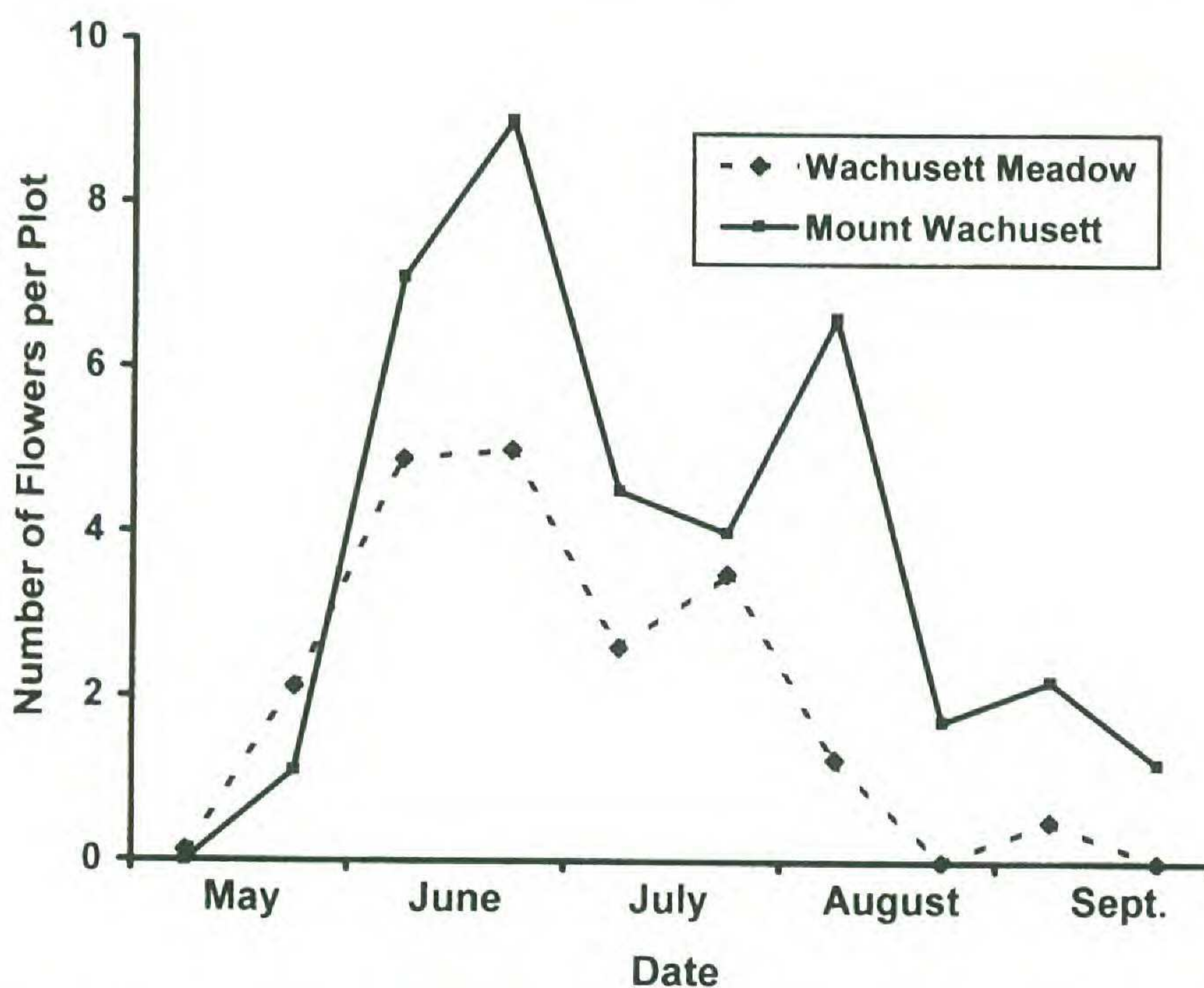


Figure 8. Flowering phenology of plants in plots A and B at Wachusett Meadow and C and D at Wachusett Mountain. Data from 1990–1998 are combined.

**Reproductive biology.** Flowering at the study sites began in mid May, peaked in June, and gradually declined through September (Figure 8), with an occasional flower as late as November.

Patterns of floral development and pollinator visitation were consistent with a high incidence of self-pollination. Flower buds enlarged to a size of about 9 mm long  $\times$  3.5 mm wide at which time the sepals separated, revealing the underlying pink corolla. Flowers usually opened overnight, with petals initially forming a cylinder around the sexual parts, and then flaring to become perpendicular to the floral axis. Fully open flowers were about 15 mm in diameter. The unopened anthers were initially pressed against the pistil and the stigmatic lobes were appressed. As the petals became fully open, the anthers moved centripetally and the lobes of the stigma separated. The stigma was presumably receptive at this time, making the flowers slightly protogynous. By mid to late morning, the five anthers of one whorl moved towards the pistil and dehisced. The anthers at this time were in contact with the stigmas and above them, covering most or all of the stigmatic surfaces with pollen. The anthers of the second whorl moved

inward and dehisced at midday or in the early afternoon. The opening of anthers in this whorl was less synchronous than the opening of anthers in the first whorl, with dehiscence of successive anthers occurring over a period of several hours, or even on successive days. The stigmatic lobes gradually diverged during anther dehiscence, though on some plants the lobes appeared to close overnight and reopen the next day. At 48 hr. from petal opening, most petals and anthers had dropped, and the stigmatic lobes were furled. Within another 24 hr. the calyx closed. The tip of the stigma extended several millimeters past the tips of the sepals at this time as a result of elongation in the 72 hr. since flower opening. After about three weeks the capsule ripened, and the five seeds were ballistically dispersed.

Pollinators were regular though not conspicuous visitors to woodland herb Robert plants, visiting during the warmer hours of sunny days. A few bumblebees (*Bombus* sp.) paused at the flowers, but contact was limited and pollen transfer was unlikely. The main visitors seen at Wachusett Meadow were small unidentified flies, roughly 9 mm in length, that appeared to be both probing for nectar and collecting pollen. In one 1.5 hr. period on a sunny afternoon, 10 of 35 observed flowers were visited by a fly, corresponding to one visit per flower per 5 hr. Assuming conditions during flowering are suitable for 5 hr. of pollinator activity during each of the two days of a flower's life, the average flower would receive roughly two visits. Visitation rates on inclement days and to isolated flowers are likely to be lower than visitation rates to concentrations of flowers on sunny days.

All flowers examined had ten ovules, although the maximum seed number was five. Anthers from Vermont plants contained an average of 72 pollen grains (SE = 4, n = 4) compared to 90 (SE = 7, n = 5) for Wachusett Mountain plants and 112 (SE = 7, n = 5) for Wachusett Meadow plants. With ten anthers per flower and assuming, as did Cruden (1977), an effective ovule number of five, the pollen/ovule ratios at these sites are 144, 180, and 224, respectively.

Hand pollinations revealed that emasculated plants rarely set fruit (9% of pollinations), while fruit set from self-pollinated, cross-pollinated, and unmanipulated flowers was high (96%, 96%, and 88%, respectively; n = 23–24 in each treatment). Isolated plants in the greenhouse also had high fruit and seed set.

## DISCUSSION

**Life cycle patterns.** Herb Robert at my study sites can be described as a facultative biennial (*sensu* Kelly 1985), or as a short-lived, monocarpic perennial. No plant flowered in the same (calendar) year it germinated and no plant survived to the year after it flowered. Over 90% of reproductive individuals flowered in their second year. The designation "winter annual" is inappropriate for these plants as they germinate mostly in the spring, and few if any reproductive individuals live for less than 12 months. References to the species as an annual in North America (Fernald 1950; Gleason and Cronquist 1991) are also incorrect for central Massachusetts plants. Geographic variation in life cycle pattern in North America is possible given the apparent variation in this characteristic among herb Robert populations in Europe (Baker 1956; Falinska and Piroznikow 1983 and references therein; Yeo 1973). Furthermore, other monocarpic species are known to exhibit an annual life cycle in warm regions and a facultative biennial life cycle in colder areas (Kalisz and Wardle 1994; Lacey 1988; Reinartz 1984)

The biennial habit is rare. Hart (1977) and Bender and Baskin (1994) used theoretical models to account for rarity. While the models differ in important details, both conclude that biennials compete successfully against plants with other life cycles only within a narrow range of juvenile and adult survivorship values. The predicted ratio of these two survivorship values must be in the vicinity of  $10^{-4}$  according to both models. In the present study, if the juvenile period extends from seedling emergence to the end of the first winter and the adult period extends from the end of the first winter to the end of the second winter and is considered only for individuals that do not flower (which inevitably results in death), the relevant survival rates are 0.07 and 0.10. These produce a ratio of 0.7, several orders of magnitude greater than predicted, suggesting that these models do not capture some key factors influencing the evolution of the biennial habit.

Several workers have commented on the habitats in which biennials are expected to occur. Hart (1977) predicted that biennials should be especially common in habitats that are neither open nor closed (e.g., midsuccessional habitats and woodland gaps). Hart further suggested that the biennial habit is appropriate for ex-

exploiting sites with intermittent resources. Schaffer and Gadgil (1975) argued that short growing seasons should favor biennials over annuals because the latter will not have time to procure enough resources for reproduction. In a similar vein, Schat et al. (1989) suggested that bienniality is advantageous in allowing production of a large stem in a short time. They contend that this is especially important in species wherein seed production is determined largely by multiple repetition of architectural units within the plant. Several workers have suggested that biennials are particularly common in early-successional habitats, disturbed habitats, and habitats unoccupied by potential competitors (Kelly 1985; Meijden and Waals-Kooi 1979; Schaffer and Gadgil 1975; Silvertown 1984; Threadgill et al. 1981). However, in an analysis of three floras, Hart (1977) reported that roughly half of the biennials were found only in natural habitats (i.e., those with minimal human influence).

Three categories of biennials were recognized by Meijden et al. (1992): transient, fugitive, and persistent. Species in the first two groups occupy disturbed or changing habitats, have short-lived populations, and produce many seeds. Persistent biennials have more persistent but fluctuating populations and relatively few seeds. All species they described in the persistent category occupy chalk grasslands. Herb Robert fits the profile of a persistent biennial reasonably well, though it is necessary to expand the habitat description beyond grasslands, perhaps to stable or closed habitats. Other woodland biennials or monocarpic perennials that might be categorized as persistent biennials include *Arabis laevigata* (Muhl.) Poiret, *Campanula americana* L., *Frasera caroliniensis* Walter, *Hydrophyllum appendiculatum* Michx., *Phacelia bipinnatifida* Michx., and *Synandra hispidula* (Michx.) Britton (Baskin and Baskin 1988; Bloom et al. 1990; Morgan 1971; Threadgill et al. 1981).

**Survival and mortality.** Twenty-six percent of hand-sown seeds emerged within 6 yr. of sowing. Survival of dispersed seeds may be higher than this if the seeds remain viable for longer than 6 yr. These figures must be interpreted cautiously since I cannot be sure that the habitats into which the seeds were sown were identical to those into which seeds are dispersed naturally.

Emergence of seedlings was heavily concentrated in early spring. The greater success of early- than of late-emerging seed-



lings could reflect the greater availability of light, water, or nutrients early in the season, or simply the longer growing season available to early-emerging plants. The pattern of emergence seen in this study seems to differ from that in some European populations of the species. In England, Roberts and Boddrell (1985) found germination to be spread more evenly through the growing season. However, by cultivating the experimental plots three times during the year, these authors may have promoted additional germination by exposing buried seeds to light. In Poland, Falinska and Piroznikow (1983) reported that groups of new offspring appeared several times during the year, though they did not indicate whether these were three entirely distinct cohorts, or parts of a continuum of germinations divided for convenience of study. The plants emerging in spring, summer, and fall differed in several aspects. As is true in my study, seedlings emerging in the spring had the highest survival rates and likelihood of flowering. Plants from the vernal cohort were invariably biennial, whereas those of the aestival cohort flowered during either their second or third year. Plants from the autumnal cohort were few in number and often did not survive to their second year.

In the present study, half of emerging seedlings did not survive to the end of the first growing season, and 87% of survivors died during the succeeding winter. General levels of mortality during both the growing season and the winter appeared to be related to weather conditions. High summer mortality was associated with low rainfall and high winter mortality with cold temperatures and little snow cover. Similar influences on winter mortality were noted for another forest biennial, *Hydrophyllum appendiculatum* (Morgan 1971). In two years, overwinter mortality decreased from 91% to 17%, with the former figure from a winter when "a period of warm temperatures [was] followed by record low temperatures with little snow cover". Short-lived plants might be especially susceptible to harsh winter conditions because they have less chance than perennials to establish a deep root system.

Two factors were related to performance of individual seedlings: emergence date and substrate depth. Plants emerging before the middle of May grew larger during their first year and had a greater chance of surviving to the end of the first growing season than did later-emerging plants. Their overwinter survival was, however, little affected by emergence time. Effects of germination time on the performance of plants are well known (Jones et al.

1997; Kalisz 1986). In most spring-germinating species, early emergence is beneficial (Miller 1987), although this may not be the case in fall-germinating species (Kalisz 1986).

Previous studies also have shown strong influences of vegetative plant size on survival and reproductive output, with large plants inevitably doing better than small plants (Gross 1981; Klinkhamer et al. 1987; Werner 1975). Vegetative size of first-year herb Robert plants influenced overwinter survival and apparently also flowering. In contrast to the typical pattern in other species, however, plants of intermediate size were most likely to survive the winter. It is not clear why larger plants did not do better than plants of intermediate size. One possibility is that the leaves (which persist through the autumn) of the largest plants may be found more often by browsing deer (which seemed to be common at both sites) during this season than those of smaller plants, which are better concealed by fallen tree leaves.

**Reproductive biology.** Herb Robert is highly self-compatible and capable of full seed set in the absence of pollinators. While experimental pollinations used plants from Vermont, it seems likely that Massachusetts plants behave similarly. The occasional fruit set observed in emasculated flowers in the laboratory was presumably due to contamination with pollen, since the small flower size made it difficult to remove the anthers cleanly and pollen grains were occasionally observed on the stigmas of flowers in this treatment.

The actual level of self-pollination in nature is unknown, but probably high. Pollen grains were often observed on stigmas in the early morning before pollinators were seen, and before there was evidence of insect removal of pollen from the anthers. The proximity of anthers and stigmas, and the infrequency of visitors, particularly during the early morning female phase before autogamy occurs, made self-pollination a virtual certainty. Baker (1953) concluded that the species was largely selfed in Great Britain, with “rarely more than 2–3% of outcrossing.”

Other aspects of herb Robert’s floral biology also suggest a predominance of selfing. Compared to its sympatric congener, *Geranium maculatum*, the flowers of *G. robertianum* are small (11–15 mm vs. 32 mm) and the pollen/ovule ratio is low (140–230 vs. 1062; Cruden 1977; Martin 1965). The former range falls between the means of Cruden’s (1977) categories of obligate au-

togamy and facultative autogamy, while the latter lies between facultative xenogamy and xenogamy.

According to reports in the literature, the reproductive biology of herb Robert is somewhat variable. Knuth (1908) reported that unisexual flowers occurred in addition to hermaphroditic ones, although none was observed in the present study. Different observers have reported the flowers to be either protandrous or homogamous (Knuth 1908), in contrast to the slight protogyny observed in Massachusetts plants. Knuth (1908) described the flowers as though cross-pollination was frequent as a result of the protandrous condition of flowers and the projection of the stigmas above the anthers. He further recorded a variety of floral visitors in Europe, including large and small bees, flies, butterflies, and beetles.

In central Massachusetts, herb Robert is predominantly a woodland biennial that grows in thin organic soils on and around boulders. Its survivorship appears to be influenced by summer droughts and cold winter periods with minimal snow cover. These factors are probably associated with the dramatic year-to-year fluctuations in abundance of reproductive plants. Self-pollination may be advantageous in such situations, allowing reproduction when density of reproductive individuals is low. Under such unpredictable conditions, seed dormancy and a seed bank are helpful in insuring survival of some offspring in the face of consecutive bad years. A strict interpretation of the species' life cycle in terms of these environmental conditions seems inappropriate because other species in the same vicinity exhibited other life history patterns. Nevertheless, herb Robert was more likely to occupy thin litter over rocks than other species. Plants in this microhabitat may be at a higher risk of mortality than species in deeper soils, and this may reduce the advantage of allocating resources to future reproduction, favoring a biennial life cycle to a perennial life cycle. The absence of an annual life cycle might reflect the difficulty in accruing sufficient resources for reproduction in a single growing season in the low light conditions of the forest floor.

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